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Genetic variance components and genetic effects among eleven diverse upland cotton lines and their F2 hybrids

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Abstract Selecting high yielding upland cotton, *Gossypium hirsutum* L. lines with improved fiber quality is a primary breeding goal. A diverse set of ten cultivars and one breeding line were crossed in a half diallel. Parents and F_2 hybrids were grown in three environments at Mississippi State, MS. Ten agronomic and fiber traits were analyzed by a mixed linear model approach based on the additive-dominance genetic model. Variance component, genetic effects and genetic correlations were calculated. 'Acala Ultima' was a desirable general combiner for fiber length, uniformity, strength, micronaire, lint percentage, and boll weight. 'FiberMax 966' was a desirable general combiner for fiber length, uniformity, strength, and all agronomic traits. 'Tamcot Pyramid' and M240 were poor general combiners for both fiber and agronomic traits. 'Coker 315' was a good general combiner for fiber length, uniformity, micronaire, boll weight, boll number, and yield. Heterozygous dominance effects were associated with several crosses, which suggest their use as hybrids.

Keywords Hybrids · Cotton · *Gossypium hirsutum* · Breeding · Genetics · Genetic variances

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Abbreviations

UHM	Mean length of upper 50% of fibers in mm
UR	Fiber uniformity ratio in %
T1	Fiber strength in kN m kg^{-1}
E1	Fiber elongation in %
MIC	Fiber micronaire
HVI	High volume instrument measurement
MINIQUE	Minimum norm quadratic unbiased estimation
AUP	Adjusted unbiased prediction

Introduction

Higher fiber quality in upland cotton (*Gossypium hirsutum* L.) is an increasing demand by industry due to the rapid development of new technology in the textile industry. Currently, high yielding upland cotton cultivars do not have all the fiber properties desired by the textile industry and cultivars with the best fiber quality are not as high in yield as desired. Thus, simultaneous genetic enhancement of multiple traits of interest is the primary task for most upland cotton breeding. To attain this important breeding goal, selecting parental lines with wide genetic diversity, evaluating these selected lines in their hybrids, and determining their genetic effects is essential for adequate progress.

The genetic properties of agronomic and fiber traits in cotton were reviewed by Meredith (1984). Recent studies of agronomic and fiber traits focused on general and specific combining ability among parental lines and their hybrids (Meredith 1990; Tang et al. 1993a, b, 1996; Cheatham et al. 2003). Due to the difficulty of producing enough F1 seeds for evaluations across multiple environments, F2 hybrids were usually used in field experiments (Meredith 1990; Tang et al. 1993a, b, 1996; Cheatham et al. 2003; Jenkins et al. 2006, 2007; Saha et al. 2006). Although the common analysis of variance approaches are applicable to parents and their F_1 hybrids from specific genetic mating designs, they are often not appropriate for the data sets including F_2 hybrids and/or backcross populations. Recently, mixed linear model approaches have been widely applied in cotton genetic studies (Wu et al. 1995; Tang et al. 1996; McCarty et al. 1998a, b, 2004a, b; Cheatham et al. 2003; Jenkins et al. 2006; Saha et al. 2006). The advantages of using the mixed model approaches include (1) their suitability for different types of data sets and (2) simultaneous calculations of variance components and genetic effects. For example, with the additive-dominance model, variance components for additive and dominance effects can be estimated and additive and dominance effects of future generations can be predicted (Wu et al. 1995; Cheatham et al. 2003; Jenkins et al. 2006; Saha et al. 2006).

We crossed ten upland cotton cultivars and one breeding line, with diverse traits of interest, in a half-diallel. The parents and their F_2 hybrids were planted in 2 years including three environments at Mississippi State. Ten agronomic and fiber traits were measured. The AD model and the mixed linear model approach were applied for data analyses, which included variance component estimation and genetic effects predictions. The objective of this research was to provide genetic information useful for cultivar or hybrid breeding program and information for development of random mating populations.

Materials and methods

Materials and experiments

Eleven parental lines were selected from different breeding programs and used in this study. They were 'Acala Ultima', developed by California Planting Cotton Seed Distributors (Shafter, CA);'Tamcot Pyramid' developed in the Multiple Adversity Resistant Program by Texas Agricultural Experiment Station, College Station, TX (Thaxton and El-Zik 2004); 'Coker 315' developed by Coker Pedigreed Seed Co. (Hartsville, SC); 'Stoneville 825' developed by Stoneville Pedigreed Seed Co. (Stoneville, MS); 'FiberMax 966' developed by Bayer Crop Science (Lubbock, TX); M240RNR a root-knot nematode resistant line developed by ARS (Shepherd et al. 1996); 'Paymaster 'HS26'a Texas High Plains cultivar developed by Paymaster Technologies, Inc. (Plainview, TX); 'Deltapine 90' developed by Delta and Pine Land Co. (Scott, MS); 'Suregrow 747' developed by the SureGrow Co. (Centre, AL); 'Phytogen PSC 355' developed by the Mississippi Agricultural and Forestry Experiment Station (Mississippi State, MS) and licensed to Phytogen Seeds (Indianapolis, IN); and 'Stoneville 474' developed by Stoneville Pedigreed Seeds. These represent a diverse group of lines from major breeding programs. Pedigrees for all except M-240 RNR (Shepherd et al. 1996) can be found in Bowman et al. (2006). A set of half diallel crosses (55) was made in the summer of 2002. F_1 seeds were sent to Mexico to produce F_2 seeds in the winter of 2003.

In 2004, 55 F_2 hybrids and their 11 parental lines were grown in two locations (environments 1 and 2, respectively) at Mississippi State (33°4′ N, 88°8′ W) In 2005, the same 66 entries were planted in one location (environment 3) at Mississippi State. In each environment plants were grown in a randomized complete block design with four replications. Plot size was a single row 12 m in length with row spacing of 0.97 m. The planting was a solid row pattern. The stand density consisted of single plants spaced $\sim$10 cm apart. The soil type in Environments 1 and 3 was a Leeper silty clay loam (Fine, smectitic, nonacid, thermic Vertic Epiaquepts). The soil type in Environment 2 was a Marietta sandy clay loam (fine-loamy, siliceous, active, thermic, Fluvaquentic Eutrudepts). Planting dates for environments 1, 2, and 3 were May 11, 2004; May 25, 2004; and May 13, 2005, respectively. Harvest dates for environments 1 and 2 were November 1, 2004 and for environment 3, October 17, 2005.

Normal field practices were followed during the season. Prior to machine harvest, a 25 boll sample for each plot was hand harvested to determine the boll weight (BW, g) and lint percentage (LP, %). Boll number was calculated by dividing seed cotton yield by boll weight. The ginned sample provided the fiber for high volume instrument (HVI) fiber trait measurement, which were made at Starlab® in Knoxville, TN. Upper Half Mean (mean length of upper 50% of fibers, UHM, mm), fiber uniformity (UR, %), fiber strength (kN m kg^{-1}), fiber elongation (EL, %), and micronaire (MIC) measurements were made. Plot seed cotton was machine picked and converted into seed cotton yield per hectare (YLD, kg ha^{-1}) and lint yield (LY, kg ha^{-1}) accordingly.

Genetic model and statistical methods

The three-environment data set was analyzed by SAS 9.0 subject to the ANOVA methods for these 66 entries. This data set was also analyzed by the AD model (Cockerham 1980), a genetic model including additive effects, dominance effects, and their corresponding G × E interaction effects (Zhu 1993; Wu et al. 1995; Tang et al. 1996; Saha et al. 2006; Jenkins et al. 2006). The genetic model regarding parents and F_2 hybrids was detailed in several previous studies (Jenkins et al. 2006). Variance components for each trait were estimated by the MINQUE (minimum norm quadratic unbiased estimation) approach (Rao 1971) with the prior values for all variance components set as 1 (MINQUE1), (Zhu 1989). Additive and dominance effects for each of ten traits were predicted by the AUP (adjusted unbiased prediction) approach and expressed as deviations from the 66 line population mean (Zhu 1993). The jackknife procedure was applied through consecutive removal of one block within each environment (Miller 1974). An appropriate *t*-test was used to detect the significance for each parameter (one-tailed test for variance components and two-tailed for predicted effects). The predicted additive and dominance effects were used to calculate the genetic correlation coefficients among traits in terms of additive effects and dominance effects. This part of the analysis was conducted by SAS 9.0 (SAS Institute 1999).

Results and discussion

Phenotypic means for parents and F2 hybrids

The mean of F_2 hybrids were greater than the mean of parents for UHM fiber length, fiber strength, boll weight, seed cotton yield, and lint yield, indicating positive middle-parent (MP) heterosis was associated with some F_2 hybrids for these traits (Table 1). The means of F_2 hybrids were generally less than parental lines for fiber elongation and lint percentage, indicating most F_2 hybrids were associated with negative heterosis for these traits. No significant differences were detected between parents and F_2 hybrids for fiber uniformity, micronaire, and boll number. The results also indicated that dominance effects might play an important role for most traits.

Acala Ultima had the longest fibers among eleven parents (Table 2). FM966 produced longer fibers than all parents except Acala Ultima and C315. Fiber of M240 was shorter than all other parents. Acala Ultima had the highest fiber length uniformity among all parents except FM966. Acala Ultima and FM966 fiber were stronger (339 and 335 k Nm kg^{-1}, respectively) than all other parents. PSC355 had greater fiber elongation than all parents except M240. Acala Ultima had the lowest micronaire (4.14) among parents. Micronaire values >5.0 are discounted in the market. Tamcot Pyramid and C315 had micronaire significantly <5.00 (4.73 and 4.57, respectively). SG747 and ST474 had micronaire significantly >5.00 (5.25 and 5.31, respectively). All parents had lint percentage significantly higher than 40% except M240 and HS26 (38.69 and 38.99%, respectively). Boll weight of Acala Ultima and FM966 was >5.00 g

Table 1 Mean fiber and agronomic values for F_2 hybrids and parents over three environments

	UHM (mm)	UR (%)	T1 (kN m kg^{-1})	EL (%)	MIC	LP (%)	BW (g)	BN (10^3)	YLD (kg ha^{-1})	LY (kg ha^{-1})
F2	28.78	83.77	294	8.12	4.88	41.63	5.28	402.5	2,119	880
Parent	28.43	83.82	291	8.24	4.90	41.80	4.91	392.1	1,916	801
LSD0.05	0.11	NS	2	0.06	NS	0.15	0.05	NS	100	41

UHM, upper half mean; UR, uniformity ratio; T1, fiber strength; EL, fiber elongation; MIC, fiber micronaire; LP, lint percentage; BW, boll weight; BN, boll number ha^{-1}; YLD, seed cotton yield; LY, lint yield

Table 2 Parent means for fiber and agronomic values over three environments

	UHM (mm)	UR (%)	T1 (kN m kg^{-1})	EL (%)	MIC	LP (%)	BW (g)	BN (10^3)	YLD (kg ha^{-1})	LY (kg ha^{-1})
Acala Ultima	30.97	85.28	339	7.98	4.14	43.19	5.39	259.9	1,403	604
Pyramid	27.24	83.31	273	8.13	4.73	41.79	4.92	270.4	1,329	554
C315	29.15	83.73	284	7.58	4.57	42.23	4.98	454.6	2,274	956
ST825	28.41	83.73	275	7.87	5.04	40.86	4.55	418.5	1,899	776
FM966	29.61	84.86	335	7.85	4.93	43.27	5.37	393.6	2,118	915
M240	26.27	82.82	297	8.75	4.91	38.69	4.90	373.5	1,825	705
HS26	27.24	82.88	282	8.45	4.93	38.99	4.90	227.9	1,148	441
DP90	28.87	83.45	296	8.13	4.91	40.76	4.65	520.0	2,419	982
SG747	28.64	84.36	264	8.65	5.25	43.75	5.04	363.3	1,851	812
PSC355	28.45	84.22	280	8.93	5.16	41.86	4.60	519.1	2,395	1,000
ST474	27.88	83.37	276	8.33	5.31	44.42	4.66	512.3	2,414	1,070
LSD0.05	0.48	0.58	10	0.25	0.20	0.64	0.23	82.3	428	178

See Table 1 for heading definitions

whereas, ST825, DP90, PSC355, and ST474 bolls were significantly <5.00 g. Boll numbers ha^{-1} were similar for DP90, PSC355, and ST 474 and about twice as many as Acala Ultima, Tamcot Pyramid, and HS26, reflecting boll size and yield differences among parents. Seedcotton yields of C315, FM966, DP90, PSC355, and ST474 were >2,000 kg ha^{-1} while Acala Ultima, Tamcot Pyramid, and HS26 seedcotton yields were significantly <2,000 kg ha^{-1}. Seedcotton and lint yields of DP90, PSC355, and ST474 were greater than all parental lines except C315, FM966, and SG747 (Table 2).

Among F_2 hybrids 53 had fibers longer than 28 mm; whereas, only three were shorter than 28 mm (Table 3). Fiber length uniformity of all hybrids was >82.00%. Fiber of 23 hybrids was stronger than 284 kN m kg^{-1}, 17 stronger than 294, 11 stronger than 304, and four stronger than 314 kN m kg^{-1}. One hybrid (FM966 × Acala Ultima), had fiber strength of 344 kN m kg^{-1}. Fiber elongation was >8.00% for 19 hybrids and <8.00% for six hybrids. Micronaire was <5.00 units for 17 and >5.00 units for only four hybrids, indicating that the majority of the hybrids had desirable micronaire. Lint percentage was significantly higher than 40.00% for 45 hybrids. One hybrid (ST474 × SG747), had lint percentage of 44.9%. Most hybrids had bolls heavier than 5.00 g. Lint yields ranged from 631 to 1,054 kg ha^{-1}.

Variance components

Estimated variance components, expressed as proportions to the phenotypic variances, are summarized in Table 4. Significant additive effects variances were detected for all traits and were larger than dominance effects for fiber length, uniformity, strength, elongation, and micronaire, indicating early selection may be applied for fiber traits (Table 4). Significant dominance effects variances were detected for all traits and were important genetic factors for lint percentage, boll weight, seed cotton and lint yield, indicating that heterosis via hybrids may be utilized for some crosses in this study. Additive × Environment variances made minor contributions (≤2%) for all traits and were only significant for fiber uniformity (1%), elongation (2%), micronaire (2%), and lint percentage (2%). This indicated additive effects for fiber quality were primarily independent of the environment in these genetic materials used in this study. Dominance × Environment effects were significant for all traits ranging from 2% (EL) to 24% (BW). This indicated the expression of dominance effects for some traits was dependent on the specific environment and magnitude of heterosis for some crosses varied among environments. Genotypic effects (sum of additive and dominance effects) were greater than G × E interaction effects (sum of A × E

Table 3 F_2 hybrid means over three environments for agronomic and fiber traits

Parents in cross	UHM (mm)	UR (%)	T1 (kN m kg^{-1})	EL (%)	MIC	LP (%)	BW (g)	BN (10^3)	YLD (kg ha^{-1})	LY (kg ha^{-1})
Pyramid × Acala	29.25	83.99	315	8.13	4.63	42.84	6.15	308.6	1,907	815
C315 × Acala	30.35	84.79	319	7.88	4.34	42.33	5.63	362.6	2,048	863
ST825 × Acala	30.14	84.73	316	8.03	4.53	42.63	5.44	340.3	1,844	785
FM966 × Acala	30.40	84.83	344	8.01	4.55	42.96	5.71	366.1	2,092	896
M240 × Acala	29.04	83.92	325	8.15	4.67	40.65	5.81	373.9	2,176	881
HS26 × Acala	29.02	84.27	316	8.19	4.60	41.24	6.04	332.8	2,003	824
DP90 × Acala	29.97	83.97	325	7.86	4.44	41.82	5.56	367.1	2,020	843
SG747 × Acala	29.91	84.44	309	8.25	4.68	42.60	5.74	413.3	2,352	1,000
PSC355 × Acala	29.40	84.51	313	8.65	4.87	42.83	5.23	420.3	2,200	939
ST474 × Acala	30.04	84.96	320	8.21	4.68	43.54	5.33	363.7	1,960	854
C315 × Pyramid	28.70	83.68	273	7.62	4.50	41.16	5.20	327.8	1,709	704
ST825 × Pyramid	28.17	83.38	272	7.78	4.88	41.89	5.09	359.1	1,809	757
FM966 × Pyramid	28.89	83.83	299	7.78	4.63	41.71	5.25	395.7	2,063	853
M240 × Pyramid	27.16	82.96	280	8.03	4.96	41.27	5.33	285.8	1,525	631
HS26 × Pyramid	27.16	82.84	290	8.45	4.98	40.59	5.43	286.8	1,565	634
DP90 × Pyramid	28.38	82.93	288	7.73	4.90	41.54	5.00	379.6	1,903	791
SG747 × Pyramid	28.15	83.23	265	7.95	4.62	41.34	4.82	362.3	1,730	711
PSC355 × Pyramid	27.90	83.38	289	8.49	5.01	41.81	4.94	398.9	1,978	823
ST474 × Pyramid	27.86	83.48	273	7.97	5.08	43.51	5.02	381.8	1,927	836
ST825 × C315	28.93	83.54	280	7.59	4.63	41.01	5.37	480.3	2,543	1,037
FM966 × C315	30.06	84.56	323	7.85	4.84	41.91	5.77	452.2	2,618	1,095
M240 × C315	28.13	83.13	323	7.90	4.82	40.37	5.76	387.5	2,254	907
HS26 × C315	29.06	83.62	295	8.03	4.84	40.00	5.74	414.5	2,382	951
DP90 × C315	29.49	83.74	293	7.63	4.58	40.34	4.99	482.0	2,416	970
SG747 × C315	29.46	83.93	289	8.02	4.83	41.83	5.43	455.8	2,470	1,032
PSC355 × C325	29.15	84.58	284	8.26	4.85	41.73	5.18	488.1	2,532	1,054
ST474 × C315	29.00	83.48	283	7.76	4.65	41.39	5.22	459.5	2,400	991
FM966 × ST825	29.82	83.99	298	7.80	4.98	41.81	5.56	460.8	2,569	1,072
M240 × ST825	28.34	83.66	276	7.66	4.85	39.91	5.14	342.3	1,759	700
HS26 × ST825	28.30	83.18	286	8.03	4.98	40.55	5.31	390.2	2,079	841
DP90 × ST825	28.91	83.17	278	7.58	4.77	41.34	4.78	451.5	2,159	891
SG747 × ST825	28.68	83.52	269	8.08	4.97	42.13	5.00	422.5	2,111	888
PSC355 × ST825	28.74	83.91	281	8.28	4.89	40.69	4.65	446.2	2,064	839
ST474 × ST825	28.41	83.69	271	7.84	5.13	42.19	4.97	427.0	2,111	890
M240 × FM966	28.24	83.31	308	7.95	4.92	40.64	5.52	399.5	2,200	892
HS26 × FM966	28.60	83.83	316	8.32	4.91	40.86	5.72	425.6	2,439	994
DP90 × FM966	29.21	83.94	313	7.81	4.78	42.23	5.14	444.9	2,330	980
SG747 × FM966	29.25	84.42	294	8.13	5.03	43.11	5.52	396.7	2,173	936
PSC355 × FM966	29.57	84.45	326	8.57	5.21	42.34	5.42	416.3	2,269	959
ST474 × FM966	29.23	84.34	305	8.14	5.22	43.53	5.37	415.9	2,240	970
HS26 × M240	27.16	82.78	279	8.27	5.11	39.30	5.40	363.7	1,957	767
DP90 × M240	27.56	82.67	290	8.03	4.91	40.65	5.09	416.1	2,101	854
SG747 × M240	27.94	83.52	283	8.45	5.17	42.24	5.57	377.7	2,109	886

Table 3 continued

Parents in cross	UHM (mm)	UR (%)	T1 (kN m kg^{-1})	EL (%)	MIC	LP (%)	BW (g)	BN (10^3)	YLD (kg ha^{-1})	LY (kg ha^{-1})
PSC355 × M240	27.77	83.47	293	8.71	5.38	41.06	4.92	428.8	2,128	875
ST474 × M240	27.60	83.01	280	8.17	4.96	41.30	5.09	408.3	2,100	867
DP90 × HS26	28.74	83.39	293	8.04	4.93	39.93	5.20	507.2	2,603	1,036
SG747 × HS26	28.47	83.91	278	8.38	5.13	40.26	5.48	339.6	1,875	755
PSC355 × HS26	28.11	83.65	296	8.60	4.95	40.02	5.04	381.4	1,902	760
ST474 × HS26	28.32	83.82	285	8.55	5.07	41.61	5.37	414.5	2,242	931
SG747 × DP90	29.04	83.43	283	8.32	5.02	42.26	4.95	384.4	1,930	814
PSC355 × DP90	29.32	83.91	304	8.60	5.15	41.51	4.67	482.1	2,254	930
ST474 × DP90	28.58	83.45	293	8.20	5.05	41.97	4.73	429.0	2,005	842
PSC355 × SG747	28.81	84.25	275	8.85	5.14	42.72	4.80	461.2	2,229	952
ST474 × SG747	28.19	83.84	273	8.52	5.22	44.19	4.85	410.4	1,990	878
ST474 × PSC355	28.74	84.42	297	8.69	5.13	42.58	4.86	445.4	2,175	921
LSD 0.05	0.48	0.58	10	0.25	0.20	0.64	0.23	82.3	428	178

See Table 1 for heading definitions

Table 4 Estimated proportional variance components for agronomic and fiber traits

Component	UHM	UR	Strength	EL	MIC	LP	BW	BN	SCY	LY
V_A/V_P	0.54**	0.31**	0.57**	0.42**	0.27**	0.33**	0.27**	0.10**	0.08**	0.08**
V_D/V_P	0.14**	0.02**	0.12**	0.19**	0.15**	0.22**	0.32**	0.03**	0.13**	0.12**
V_{AE}/V_P	0.00	0.01**	0.00**	0.02**	0.02**	0.02**	0.00	0.00	0.00	0.00**
V_{DE}/V_P	0.03**	0.14**	0.06**	0.02**	0.16**	0.20**	0.24**	0.17**	0.18**	0.18**
V_e/V_P	0.29**	0.52**	0.24**	0.36**	0.40**	0.23**	0.17**	0.70**	0.61**	0.62**

See Table 1 for heading definitions

V_A = additive variance; V_D = dominance variance; V_{AE} = additive by environment variance; V_{DE} = dominance by environment variance; V_e = error variance; V_P = phenotypic variance

* Significant at probability level of 0.05

** Significant at probability level of 0.01

or D × E effects) for fiber length (68 vs. 3%), uniformity (33 vs. 15%), fiber strength (69 vs. 6%), fiber elongation (61 vs. 4%), micronaire (42 vs. 18%), lint percentage (55 vs. 22%), and boll weight (59 vs. 24%). This indicated the effect of these environments on these traits was low. Contrarily, both genotypic effects and G × E interaction effects played a similar role for boll number (13 vs. 17%), seed cotton yield (21 vs. 18%), and lint yield (20 vs. 18%), suggesting that genetic expression for these three traits was highly dependent on specific environments. Residual error also made important contributions to the phenotypic variances and varied among traits from 17% (boll weight) to 70% (boll number) with the largest effects on yield and boll number (Table 4).

Additive effects

Additive effects, which are equivalent to general combining ability under the AD genetic model, are important genetic information for determining desirable general combiners for improving traits of interest. The predicted additive effects are summarized in Table 5. Positive and negative additive effects were about equally divided among parents for all traits except fiber strength and boll number.

Table 5 Predicted additive genetic effects for 11 parents for fiber and agronomic traits

Parent	UHM (mm)	UR (%)	Strength (kN m kg^{-1})	EL (%)	MIC	LP (%)	BW (g)	BN (10^3)	SC (Kg ha^{-1})	LY (Kg ha^{-1})
Acala Ultima	1.01**	0.71**	29.4**	0.05**	−0.27**	0.75**	0.43**	−32.28**	−16*	8**
Pyramid	−0.69**	−0.47**	−11.0**	−0.16**	−0.06**	0.17**	−0.07**	−53.27**	−288**	−116**
C315	0.52**	0.18 **	−2.8**	−0.28**	−0.21**	−0.58**	0.18**	28.49**	211**	76**
ST825	0.09**	−0.12**	−13.4**	−0.29**	−0.04**	−0.17**	−0.14**	8.95**	−14**	−9**
FM966	0.59**	0.37**	19.7**	−0.07**	0.03**	0.44**	0.22**	18.13**	183**	84**
M240	−0.93**	−0.59**	−5.0**	−0.05**	0.11**	−0.79**	0.10**	−27.61**	−90**	−51**
HS26	−0.51**	−0.22**	−0.2	0.19**	0.08**	−1.21**	0.24**	−3.41**	58*	0
DP90	0.14**	−0.37**	1.7**	−0.17**	−0.04**	−0.23**	−0.30**	25.76**	12*	0
SG747	−0.01	0.04**	−14.3**	0.18**	0.08**	0.59**	−0.09**	2.93*	−19**	5
PSC355	−0.04**	0.32**	3.6**	0.50**	0.19**	0.12**	−0.35**	28.90**	15*	9**
ST474	−0.18**	0.15**	−7.6**	0.10**	0.13**	0.91**	−0.22**	3.43*	−52**	−6

See Table 1 for heading definitions

* Significant at probability level of 0.05

** Significant at probability level of 0.01

They ranged from negative 0.93 to positive 1.01 mm for UHM. Additive effects for uniformity varied <1% among parents. Fiber strength effects varied from −14.3 to 29 kN m kg^{-1}. Additive effects for percent elongation varied <1%. Additive effects for micronaire varied from −0.27 to 0.19. Interestingly, the additive effect of Acala Ultima reduced micronaire by −0.27, which could be very useful. There were useful additive effects for increased lint percentage with the highest value being 0.91% for ST474. Acala Ultima had the heaviest boll and it contributed significant additive effects of 0.43 g to boll weight. As expected, several parents with lighter bolls contributed positive additive effects to boll number and several with heavier bolls contributed negative additive effects to boll number. Additive effects for lint yield ranged from −116 (Pyramid) to 84 (FM966) kg ha^{-1}.

Summarizing additive effects, Acala Ultima was a desirable general combiner for fiber length, uniformity, strength, micronaire, lint percentage and boll weight. FM966 was a good general combiner for fiber length, uniformity, strength, and all agronomic traits. However, Tamcot Pyramid and M240 were poor general combiners for most agronomic traits. C315 was a good general combiner for fiber length, uniformity, micronaire, boll weight, boll number, and yield.

Dominance effects

Two types of dominance effects, homozygous (Table 6) and heterozygous dominance effects (Table 7) were predicted. Homozygous dominance effects are related to inbreeding depression following the selfing of hybrids. The more negative the homozygous dominance effects for a parent, the greater the amount of inbreeding depression expected when this parent is used in crosses, followed by selfing. The large number of parents with negative homozygous dominance for fiber length, strength, and boll weight indicates we should expect inbreeding depression in several crosses in later generations of self pollination.

Heterozygous effects are related to specific combining ability for the pair of parents in a cross. Table 7 shows the parents with positive and negative homozygous dominance effects. There was an even distribution of negative and positive heterozygous dominance effects in the F_2 hybrids, except for UHM which had 31 positive and 18 negative and boll weight which had 34 positive and 21 negative (Table 7). Thus positive or negative hybrid vigor was shown for most traits among the F_2 hybrids. A few specific hybrids stood out as desirable for specific traits. FM966 × C315, PSC355 × FM966, and ST474 × PSC355 were best for strength. PSC355 × Tamcot Pyramid had reduced micronaire of 0.46.

Table 6 Predicted homozygous dominance genetic effects for agronomic and fiber traits

Parent	UHM (mm)	UR (%)	T1 (kN m kg^{-1})	EL (%)	MIC	LP (%)	BW (g)	BN	YLD (Kg ha^{-1})	LY (Kg ha^{-1})
Acala Ultima	0.13**	0.06**	−9.2**	−0.15**	−0.15**	0.16**	−0.93**	−28.1**	−535**	−218**
Pyramid	−0.39**	0.14**	−2.0**	0.33**	−0.01	−0.08**	−0.41**	−9.4**	−174**	−71**
C315	−0.69**	−0.11**	−5.7**	0.04**	0.08**	1.70**	−0.84**	−3.5	−280**	−84**
ST825	−0.64**	0.06**	3.9**	0.33**	0.20**	−0.33**	−0.63**	−2.0	−198**	−81**
FM966	−0.39**	0.11**	2.5**	−0.08**	0.01	0.79**	−0.54**	−16.9**	−344**	−124**
M240	−0.85**	0.05**	9.2**	0.72**	−0.15**	−1.22**	−0.77**	7.1**	−133**	−66**
HS26	−0.68**	−0.14**	−11.2**	0.02	−0.08**	−0.18**	−1.05**	−58.0**	−822**	−314**
DP90	−0.30**	0.11**	−3.0**	0.37**	0.09**	−0.31**	−0.20**	19.8**	120**	42**
SG747	−0.26**	0.16**	−4.1**	0.23**	0.17**	0.97**	−0.24**	−17.2**	−226**	−78**
PSC355	−0.38**	−0.04**	−19.1**	−0.09**	−0.07**	0.08	−0.16**	19.5**	100**	41**
ST474	−0.66**	−0.19**	−6.0**	0.08**	0.15**	1.00**	−0.37**	34.7**	216**	109**

See Table 1 for heading definitions

* Significant at probability level of 0.05

** Significant at probability level of 0.01

M240 × Tamcot Pyramid, DP90 × M240, SG747 × M240, and ST474 × SG747 had >0.80% increase in lint percentage. It is significant that three parents, in crosses with the low lint percentage root-knot resistant parent M240, increased the lint percentage. The F_2 hybrid from big boll parents Acala Ultima and Tamcot Pyramid showed a 1.11 g heterozygous dominance effect for boll weight. Heterozygous dominance effects for boll number increased in several crosses translating into increases in yield. Heterozygous dominance effects were >100 kg ha^{-1} for 7 F_2 hybrids. The highest heterozygous dominance effect was 245 kg ha^{-1} for the F_2 hybrid of DP90 × HS26.

Correlation analysis among traits in terms of additive and dominance effects

Predicted additive effects and dominance effects were used to calculate the correlation coefficients among these ten traits. The results are summarized in Tables 8 and 9. Additive effects for fiber length were positively correlated with fiber uniformity (0.84), fiber strength (0.67), seed cotton yield (0.61), and lint yield (0.72), and negatively with micronaire (−0.62, Table 8). Fiber uniformity was positively correlated with fiber strength (0.67) and lint yield (0.65). Fiber elongation had significant additive correlation with micronaire (0.61). Boll number had similar additive correlation coefficients with seed cotton yield (0.77) and lint yield (0.76).

Dominance effects correlations were significant but generally low except boll number with yield. Fiber length was positively correlated with uniformity (0.45), fiber strength (0.25), boll weight (0.43), and seed cotton yield (0.24), and negatively with fiber elongation (−0.26, Table 9). Fiber strength was positively correlated with fiber elongation (0.48), micronaire (0.28), and boll weight (0.34) for dominance effects. Elongation had positive dominance correlation with micronaire (0.42). Micronaire was positively correlated with lint percentage (0.56) and boll weight (0.29) for dominance effects. Boll weight had significant correlation with boll number (0.26) and correlations with seed cotton yield and lint yield were 0.63. Boll number was highly correlated with seed cotton yield (0.91) and lint yield (0.89).

Conclusions

Our results show that several parents were associated with desirable additive effects for fiber quality and/or yield and thus can be used as good general combiners for developing cultivars with improvement in multiple traits. For example, Acala Ultima was a desirable general combiner for fiber length, uniformity, strength, micronaire, lint percentage, and boll weight and

Table 7 Predicted heterozygous dominance genetic effects for agronomic and fiber traits

Parents in cross	UHM (mm)	UR (%)	T1 ($kN\ m\ kg^{-1}$)	EL (%)	MIC	LP (%)	BW (g)	BN	YLD ($kg\ ha^{-1}$)	LY ($kg\ ha^{-1}$)
Pyramid × Acala	0.10**	−0.06**	7.4**	0.22**	0.20**	0.59**	1.11**	7.7**	316**	135**
C315 × Acala	0.15**	0.11**	3.4**	0.10**	−0.04**	0.30**	−0.10**	−12.3**	−155**	−56**
ST825 × Acala	0.44**	0.18**	10.2**	0.26**	−0.05**	0.90**	0.06**	−14.2**	−129**	−38**
FM966 × Acala	0.00	−0.05**	6.3**	0.04**	−0.05**	0.00	−0.16**	1.6	−37*	−12*
M240 × Acala	0.31**	−0.01	10.8**	−0.08**	0.05**	−1.01**	0.32**	25.8**	357**	126**
HS26 × Acala	−0.42**	0.05**	−2.5**	−0.11**	−0.02**	0.25**	0.60**	11.0**	211**	86**
DP90 × Acala	−0.03	−0.13**	5.4**	−0.22**	−0.14**	−0.35**	0.40**	−18.0**	−73**	−30**
SG747 × Acala	0.08**	−0.10**	3.3**	−0.08**	−0.02*	−0.92**	0.35**	40.0**	511**	196**
PSC355 × Acala	−0.64**	−0.13**	−9.8**	0.19**	0.20**	0.61**	−0.13**	14.4**	152**	72**
ST474 × Acala	0.69**	0.25**	11.2**	0.04**	−0.06**	0.09**	−0.10**	−12.3**	−98**	−36**
C315 × Pyramid	0.27**	0.10**	−11.6**	−0.19**	−0.18**	−0.59**	−0.18**	−27.2**	−338**	−137**
ST825 × Pyramid	0.06**	0.03	−2.2**	−0.01	0.08**	0.74**	0.14**	2.6	59**	34**
FM966 × Pyramid	0.35**	−0.01	−7.6**	−0.22**	−0.29**	−1.03**	−0.29**	25.8**	158**	41**
M240 × Pyramid	0.06**	0.05**	−4.23**	−0.15**	0.11**	1.07**	0.17**	−23.2**	−209**	−63**
HS26 × Pyramid	−0.64**	−0.14**	13.4**	0.44**	0.15**	0.23**	0.21**	−10.7**	−91**	−29**
DP90 × Pyramid	0.19**	−0.11**	3.6**	−0.30**	0.15**	0.24**	0.09**	−3.3*	17	15*
SG747 × Pyramid	0.03	−0.17**	−8.8**	−0.44**	−0.46**	−1.96**	−0.60**	14.9**	−20	−39**
PSC355 × Pyramid	−0.28**	−0.16**	9.6**	0.05**	0.04**	−0.03	0.06**	6.7**	110**	40**
ST474 × Pyramid	−0.03	0.04**	−5.8**	−0.23**	0.15**	1.10**	0.04*	4.8	94**	48**
ST825 × C315	−0.43**	−0.13**	0.3	−0.02	−0.10**	−0.18**	0.35**	23.6**	317**	117**
FM966 × C315	0.51**	0.14**	18.6**	0.21**	0.18**	−0.15**	0.36**	4.9**	193**	78**
M240 × C315	−0.09*	−0.10**	9.2**	−0.05**	0.08**	0.12*	0.66**	−14.2**	41	14
HS26 × C315	0.70**	0.05**	6.9**	0.06**	0.13**	−0.21**	0.49**	12.2**	264**	95**
DP90 × C315	0.25**	0.09**	−4.3**	−0.16**	−0.13**	−1.20**	−0.20**	6.0**	1	−21**
SG747 × C315	0.42**	−0.04	10.3**	−0.03*	0.02	−0.59**	0.21**	17.8**	242**	90**
PSC355 × C315	0.01	0.24**	−11.2**	−0.02	−0.01	0.37**	0.20**	6.9**	146**	65**
ST474 × C315	0.09**	−0.20**	−12.6**	−0.26**	−0.29**	−1.87**	0.11**	0.6	31	−16*
FM966 × ST825	0.77**	−0.07**	−7.5**	0.04**	0.09**	−0.20**	0.50**	22.9**	409**	161**
M240 × ST825	0.88**	0.26**	−8.5**	−0.54**	−0.15**	−0.52**	0.05**	−29.4**	−289**	−119**
HS26 × ST825	0.11**	−0.10**	7.7**	−0.03	0.04**	0.82**	0.21**	10.4**	171**	76**
DP90 × ST825	−0.04	−0.14**	−10.6**	−0.33**	−0.15**	0.57**	−0.08**	−2.8	−38*	−5
SG747 × ST825	−0.20**	−0.16**	−1.2**	−0.01	−0.07**	0.02	−0.05*	9.9**	79**	31**

Table 7 continued

Parents in cross	UHM (mm)	UR (%)	T1 (kN m kg^{-1})	EL (%)	MIC	LP (%)	BW (g)	BN	YLD (kg ha^{-1})	LY (kg ha^{-1})
PSC355 × ST825	−0.01	−0.03*	−2.0**	−0.09**	−0.24**	−1.24**	−0.25**	−6.5**	−150**	−78**
ST474 × ST825	−0.23**	0.01	−6.5**	−0.22**	0.11**	−0.42**	0.18**	−9.1**	−45**	−24**
M240 × FM966	−0.14**	−0.19**	−6.5**	−0.25**	−0.08**	−0.77**	0.03*	5.5*	40	1
HS26 × FM966	−0.27**	−0.04*	5.8**	0.25**	−0.07**	−0.12**	0.24**	30.5**	397**	149**
DP90 × FM966	−0.42**	0.00	−3.89**	−0.15**	−0.16**	0.59**	−0.14**	−4.5**	−39	−4
SG747 × FM966	−0.14**	0.03**	−9.5**	−0.12**	−0.01	0.19**	0.17**	−6.6**	−56**	−17*
PSC355 × FM966	0.46**	−0.01	19.3**	0.20**	0.19**	0.05	0.44**	−25.3**	−114**	−43**
ST474 × FM966	0.24**	0.08**	−1.8*	0.08**	0.21**	0.34**	0.18**	−13.4**	−100**	−35**
HS26 × M240	−0.09**	−0.06	−17.8*	−0.18**	0.15**	0.11**	−0.03*	12.9**	98**	38**
DP90 × M240	−0.57**	−0.15	−6.5**	−0.14**	−0.03**	0.80**	0.08**	−3.8+	−29*	2
SG747 × M240	0.24**	0.07	6.1**	0.06**	0.13**	1.57**	0.57**	0.9	155**	79**
PSC355 × M240	0.07**	−0.02	2.2**	0.09**	0.37**	0.75**	−0.16**	0.7	4	13
ST474 × M240	0.12**	−0.12	−8.0**	−0.22**	−0.22**	−0.53**	−0.01	−0.4	18	−2
DP90 × HS26	0.62**	0.11	−0.1	−0.22**	0.01	−0.13**	0.14**	61.8**	651**	245**
SG747 × HS26	0.38**	0.17	−0.4	−0.17**	0.10**	−1.43**	0.27**	−11.2**	−63**	−44**
PSC355 × HS26	−0.09**	−0.03	8.3**	−0.20**	−0.22**	−0.69**	−0.09**	−15.6**	−203**	−91**
ST474 × HS26	0.56**	0.20	0.8*	0.30**	−0.05**	0.25**	0.36**	13.6**	260**	103**
SG747 × DP90	0.17**	−0.10	2.4**	0.17**	0.04**	0.32**	−0.02+	−33.7**	−303**	−115**
PSC355 × DP90	0.70**	0.09	14.0**	0.25**	0.17**	0.22**	−0.09**	−4.1	−78*	−30**
ST474 × DP90	−0.15**	−0.01	7.4**	0.17**	0.03*	−0.69**	−0.14**	−27.2**	−336**	−141**
PSC355 × SG747	0.10**	0.03	−7.3**	0.15**	−0.05**	0.36**	−0.23**	11.8**	69**	36**
ST474 × SG747	−0.56**	−0.03	0.0	0.19**	0.06**	1.13**	−0.29**	−7.9**	−178**	−58**
ST474 × PSC355	0.41**	0.21	18.2**	0.08**	−0.13**	−0.42**	0.16**	−17.1**	−124**	−59**

See Table 1 for heading definitions

* Significant at probability level of 0.05

** Significant at probability level of 0.01

Table 8 Correlation coeffients for additive genetic effects among agronomic and fiber traits

	UR	T1	EL	MIC	LP	BW	BN	YLD	LY
UHM	0.84**	0.67*	−0.12	−0.62*	0.45	0.34	0.38	0.61*	0.72**
UR		0.67*	0.32	−0.30	0.58	0.32	0.28	0.50	0.65*
T1			0.15	−0.39	0.24	0.58	0.00	0.39	0.45
EL				0.61*	0.19	−0.19	0.11	−0.03	0.01
MIC					−0.06	−0.55	0.20	−0.15	−0.16
LP						−0.16	−0.08	−0.18	−0.05
BW							−0.36	0.31	0.28
BN								0.77**	0.76**
YLD									0.97**

See Table 1 for heading definitions

* Significant at probability level of 0.05

** Significant at probability level of 0.01

Table 9 Correlation coefficients for dominance genetic effects among agronomic and fiber traits

	UR	T1	EL	MIC	LP	BW	BN	YLD	LY
UHM	0.45**	0.25*	−0.26*	−0.03	−0.21	0.43**	0.04	0.24*	0.21
UR		0.17	0.19	0.10	0.07	0.03	−0.17	−0.12	−0.12
T1			0.48**	0.28*	0.02	0.34**	0.00	0.11	0.11
EL				0.42**	0.23	−0.07	0.00	−0.01	0.02
MIC					0.56*	0.29*	0.03	0.15	0.22
LP						0.05	−0.11	−0.06	0.05
BW							0.26**	0.63**	0.63**
BN								0.91**	0.89**
YLD									0.99**

See Table 1 for heading definitions

* Significant at probability level of 0.05

** Significant at probability level of 0.01

FiberMax 966 for fiber length, uniformity, strength, and all agronomic traits. Coker 315 was a good general combiner for fiber length, uniformity, micronaire, boll weight, boll number, and yield. In addition, some hybrids had desirable heterozygous dominance effects, which can be used for hybrid development. In some parts of the world breeders are developing hybrids for growers. The many heterozygous dominance genetic effects for both fiber quality traits and lint yield should be useful to these breeders. Several important and favorable additive correlations were found, e.g. fiber strength with length and uniformity, but not with lint yield. Also lint yield was not correlated with micronaire, lint percentage or boll weight, yet there was a positive correlation between lint yield and boll number. These correlations or lack of correlations will be a very important consideration in using these lines as parents. The additive correlations show that a breeder should be able to simultaneously improved fiber quality and lint yield in cultivar development. These results also suggest that a random mating approach should allow for the combining of favorable genes from multiple parents. Random mating should capture both additive and dominance variation and by allowing many recombination events to take place should provide germplasm with new combinations of alleles that should be useful in breeding. A random mating population has been developed and registered with Crop Science Society of America (Jenkins et al. 2008).

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References

Bowman DT, Gutierrez OA, Percy RG, Calhoun DS, May OL (2006) Pedigrees of upland and pima cotton cultivars released between 1970 and 2005. Bulletin 1155, Mississippi Agricultural and Forestry Experiment Station, 57 p

Cheatham CL, Jenkins JN, McCarty JC Jr, Watson CE, Wu J (2003) Genetic variance and combining ability of crosses of American cultivars, Australian cultivars, and wild cottons. J Cotton Sci 7:16–22

Cockerham CC (1980) Random and fixed effects in plant genetics. Theor Appl Genet 56:119–131

Jenkins JN, Wu J, McCarty JC Jr, Saha S, Gutierrez OA, Hayes R, Stelly D (2006) Genetic effects of thirteen *Gossypium barbadense* L. chromosome substitution lines in topcrosses with upland cultivars: I. Yield and yield components. Crop Sci 46:1169–1178

Jenkins JN, Wu J, McCarty JC Jr, Saha S, Gutierrez OA, Hayes R, Stelly D (2007) Genetic effects of thirteen *Gossypium hirsutum* L. chromosome substitution lines in topcrosses with upland cultivars: II. Fiber quality traits. Crop Sci 47:561–572

Jenkins JN, McCarty JC Jr, Gutierrez OA, Hayes RW, Bowman DT, Watson CE, Jones DC (2008) Registration of RMUP-C5, a random mated population of Upland cotton germplasm. J Plant Regist 2(3):239–242

McCarty JC Jr, Jenkins JN, Zhu J (1998a) Introgression of day-neutral genes in primitive cotton accessions: I. Genetic variances and correlations. Crop Sci 38:1425–1428

McCarty JC Jr, Jenkins JN, Zhu J (1998b) Introgression of day-neutral genes in primitive cotton accessions: II. Predicted genetic effects. Crop Sci 38:1428–1431

McCarty JC Jr, Jenkins JN, Wu J (2004a) Primitive accession germplasm by cultivar crosses as sources for cotton improvement I: phenotypic values and variance components. Crop Sci 44:1226–1230

McCarty JC Jr, Jenkins JN, Wu J (2004b) Primitive accession derived germplasm by cultivar crosses as sources for cotton improvement: II. Genetic effects and genotypic values. Crop Sci 44:1231–1235

Meredith WR (1984) Quantitative genetics. In: Kohel RJ, Lewis CF (eds) Cotton. ASA, CSSA, and SSSA, Madison, pp 131–150

Meredith WR (1990) Yield and fiber-quality potential for second generation hybrids. Crop Sci 30:1045–1048

Miller RG (1974) The jackknife: a review. Biometrika 61:1–15

Rao CR (1971) Estimation of variance and covariance components MINQUE theory. J Multivar Anal 1:257–275

Saha S, Jenkins JN, Wu J, McCarty JC Jr, Gutiérrez OA, Percy RG, Cantrell RG, Stelly D (2006) Effects of chromosome-specific introgression in upland cotton on fiber and agronomic traits. Genetics 172:1927–1938

SAS Institute (1999) SAS software version 9.0. SAS Institute, Cary

Shepherd RL, McCarty JC Jr, Jenkins JN, Parrott WL (1996) Registration of nine cotton germplasm lines resistant to root knot nematode. Crop Sci 36:820

Tang B, Jenkins JN, McCarty JC Jr, Watson CE (1993a) F2 hybrids of host plant germplasm and cotton cultivars: I. Heterosis and combining ability for lint yield and yield components. Crop Sci 33:700–705

Tang B, Jenkins JN, McCarty JC Jr, Watson CE (1993b) F2 hybrids of host plant germplasm and cotton cultivars: II. Heterosis and combining ability for fiber properties. Crop Sci 33:706–710

Tang B, Jenkins JN, Watson CE, McCarty JC Jr, Creech RG (1996) Evaluation of genetic variances, heritabilities, and correlations for yield and fiber traits among cotton F_2 hybrid populations. Euphytica 91:315–322

Thaxton PM, El-Zik KM (2004) Registration of Tamcot Pyramid. Crop Sci 44:343

Wu J, Zhu J, Xu F, Ji D (1995) Analysis of genetic effect × environment interactions for yield traits in upland cotton (Chinese). Heredita 17(5):1–4

Zhu J (1989) Estimation of genetic variance components in the general mixed model. PhD dissertation, North Carolina State University, Raleigh, USA (Diss Abstr: DA8924291)

Zhu J (1993) Methods of predicting genotype value and heterosis for offspring of hybrids. J Biomath 8(1):32–44 (Chinese)